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HERMAPHRODITISM AMONG NORTH AMERICAN FRESHWATER MUSSELS¹

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ABSTRACT

Information on the extent of hermaphroditism among the freshwater mussels of the rich naiad fauna of the U.S.A. is fragmentary. In this study the gonads of 1,871 specimens belonging to 97 species in 32 genera were histologically examined, using the paraffin block technique for sectioning. Only 4 species in 2 unionid subfamilies were shown to be dominantly hermaphroditic (monoecious); 3 in the Anodontinae: *Anodonta imbecillis*, *Lasmigona compressa* and a close relative *L. subviridis* and 1 in the Lampsilinae: *Carunculina parva*.

Sporadic hermaphrodites were found in another 22 species or forms belonging to 17 genera in 2 families. Usually such individuals appear to be predominantly of one sex, with only a small amount of gonad tissue of the opposite sex. One ambisexual specimen was found in the Margaritanidae, in *Margaritifera margaritifera*, among 24 specimens sectioned representing 2 genera and species. In the Unionidae accidentally monoecious individuals occurred in all 3 subfamilies. Among the Unioninae, with 567 specimens (34 species, 11 genera) examined such individuals were found in 9 species (or forms) of 5 genera, i.e., in *Elliptio dilatatus*, *E. productus*, *Fusconaia eburnus*, *F. flava*, *Gonidea angulata*, *Pleurobema cordatum*, *P. c. coccineum*, *Quadrula quadrula* and *Tritogonia verrucosa*. In the Anodontinae, with a total of 479 specimens (20 species, 5 genera) sectioned, sporadic hermaphrodites were demonstrated in 5 species belonging to 4 genera, of which 2 are the genera also containing the predominantly hermaphroditic species; i.e., they occurred in: *Anodonta corpulenta*, *A. grandis footiana* and *Lasmigona complanata* as well as in *Alasmidonta marginata* and *Strophitis rugosus*. In the Lampsilinae, with a total of 801 specimens (41 species, 14 genera) sectioned, the condition was detected in 7 further species representing 6 genera, i.e., in: *Actinonaias ellipsiformis*, *Lampsilis cariosa*, *Leptodea laevissima*, *Proptera alata*, *Ptychobranchus fasciolaris*, *P. subtentum* and *Villosa (Micro-myia) iris*.

This rather extensive survey of American naiades shows that they are generally dioecious. Whether or not hermaphroditism appears in animals confronted with difficult environmental conditions, as has been previously suggested, remains an open question.

One of the best summary analyses of sexual differentiation among pelecypod mollusks was published by Coe (1943). He indicated that among the 10,000 odd species of bivalves about 400 were known to deviate from the strictly dioecious or

unisexual condition and stressed that in these every grade of sexual differentiation and of ambisexuality was found. Hermaphroditism could be complete, partial or occasional. Among the normally hermaphroditic (ambisexual, mo-

¹This paper was read at the Second European Malacological Congress, Copenhagen, August, 1966 and abstracted in *Malacologia*, 1966. It has now been brought up to date in minor details.

noecious) marine species studied, some exhibited alternative sexual phases, including functional hermaphroditism. Not only could species of the same genus differ considerably in sexuality but there existed variability in different individuals of the same species or in single individuals at different periods of life. Similarly, the distribution of ovogenic and spermatogenic tissues also showed great variation. The observed variability is attributed to the interplay between multiple hereditary sex differentiating mechanisms and environmental factors, though evidence as to the influence of the latter yet needed further and more direct experimental proof.

As regards freshwater mussels, the sphaeriids are all known to be hermaphroditic, but relatively little is known about the extent of hermaphroditism in the larger forms. As late as 1926, Pelseneer noted that the number of freshwater mussels investigated in this respect was not great. That the unionid *Anodonta* may show the condition has been known for a long time. Weisensee (1916), in a scholarly article on the sex of *Anodonta*, thoroughly reviews the observations made since the time of Leeuwenhoek in 1722: he states (on p 275):

"Seit der Arbeit von Lacaze-Duthiers über den Genitalapparat der Lamellibranchiaten wurde die Frage nach der Geschlechtsverteilung bei *Anodonta* nicht mehr zum Gegenstand eingehenderer Untersuchungen gemacht. Seit diesem Zeitpunkt war man der Ansicht - und diese Ansicht finden wir in fast allen heutigen Lehrbüchern vertreten - dass sowohl *Anodonta* als auch *Unio* in der Regel getrenntgeschlechtlich seien."²

²Translation: "Since Lacaze-Duthiers' [1894] work on the genital apparatus of the lamellibranchs, the question of sex distribution in *Anodonta* has not been made the object of further detailed investigation. The general view held since that time - a view to be found in almost all textbooks today - is that *Anodonta*, as well as *Unio*, are, as a rule, of separate sexes."

Hermaphroditism in British *Anodonta* was intensively studied by Bloomer (1930, 1934, 1935, 1939). Pelseneer (1920) quotes Schierholz's report of *Margaritifera* as an occasional hermaphrodite in Germany. In the U.S.A. Sterki (1898) recognized hermaphroditism in 3 unionids: *Anodonta imbecillis*, *Carunculina parva* and *Fusconaia flava*. In the latter 2 genera for the first time Ortman (1912) noted, however, that most of the Unioninae have separate sexes. The histology of the gonads of *Carunculina parva* was later studied by Tepe (1943).

The aim of the present study was to investigate the extent of hermaphroditism among the numerous species of freshwater mussels (Unionacea) and, if possible, to gain information on factors that may serve to induce hermaphroditism. During the past several years material was collected from widely distributed locations, and 1,871 specimens belonging to 97 species (or forms) in 32 genera (Table 1) were histologically examined. The distribution of these species as to family group was as follows: 2 species in the Margaritanidae; and, in the Unionidae, 34 species in the Unioninae, 20 in the Anodontinae and 41 in the Lampsilinae.

The specimens were anaesthetized (usually in sodium nembutal) and killed and fixed (mostly in Bouin's fluid). They were then serially sectioned in paraffin and stained with haematoxylin and eosin.³

RESULTS

In the present study, only 4 unionid species have been found to be dominantly hermaphroditic (Tables 1, 2), while sporadic, sometimes partial hermaphrodites were found in 22 species distributed in all families and subfamilies (Tables 1,

³The investigation is continuing. To date another 2000 specimens have been quick frozen and sectioned with a cryostat (a microtome designed to cut frozen tissue). So far, no essential differences from the results reported in this paper have been found.

TABLE 1. North American freshwater mussels sectioned to determine sex (97 species; 32 genera)

Species	Nos. sectioned
MARGARITANIDAE (2 species; 2 genera)	
<i>Cumberlandia monodonta</i> (Say)	12
* <i>Margaritifera margaritifera</i> (Linnaeus)	12
	24
UNIONIDAE (95 species; 30 genera)	
Unioninae (34 species; 11 genera)	
<i>Amblema boykiniana</i> (Lea)	5
<i>Amblema costata</i> (Rafinesque)	15
<i>Amblema costata plicata</i> (Say)	1
<i>Amblema neislerii</i> (Lea)	6
<i>Amblema peruviana</i> (Lamarck)	1
<i>Amblema perplicata</i> (Conrad)	6
<i>Cyclonaias tuberculata</i> (Raf.)	20
<i>Elliptio buckleyi</i> (Lea)	6
<i>Elliptio complanatus</i> (Dillwyn)	5
<i>Elliptio crassidens</i> (Lamarck)	22
* <i>Elliptio dilatatus</i> (Raf.)	68
<i>Elliptio fraternus</i> (Lea)	8
* <i>Elliptio productus</i> (Conrad)	9
<i>Elliptio sloatianus</i> (Lea)	6
<i>Elliptio strigosus</i> (Lea)	6
<i>Elliptio tuomyi</i> (Lea)	6
<i>Fusconaia barnesiana</i> (Lea)	6
* <i>Fusconaia ehenus</i> (Lea)	35
* <i>Fusconaia flava</i> (Raf.)	68
<i>Fusconaia succissa</i> (Lea)	34
* <i>Gonidea angulata</i> (Lea)	12
<i>Lexingtonia dolabelloides</i> (Lea)	7
<i>Megaloniaias gigantea</i> (Barnes)	2
<i>Plethobasus cooperianus</i> (Lea)	1
<i>Plethobasus cyphus</i> (Raf.)	1
* <i>Pleurobema cordatum</i> (Raf.)	38
* <i>Pleurobema cordatum coccineum</i> (Conrad)	35
<i>Pleurobema pyriforme</i> (Lea)	8
<i>Pleurobema strodeanum</i> (B. H. Wright)	7
<i>Quadrula cylindrica</i> (Say)	4
<i>Quadrula pustulosa</i> (Lea)	23
* <i>Quadrula quadrula</i> (Raf.)	85
<i>Quadrula quadrula speciosa</i> (Lea)	2
* <i>Tritogonia verrucosa</i> (Raf.)	9
	567
Anodontinae (20 species; 5 genera)	
<i>Alasmidonta calceolus</i> (Lea)	86
* <i>Alasmidonta marginata</i> (Say)	48
<i>Alasmidonta undulata</i> (Say)	4
<i>Anodonta couperiana</i> Lea	6

Table 1 (contd.)

Species	Nos. sectioned
Anodontinae (contd.)	
* <i>Anodonta corpulenta</i> Cooper	35
<i>Anodonta californiensis</i> Lea	6
* <i>Anodonta grandis footiana</i> (Lea)	12
<i>Anodonta cataracta</i> Say	2
<i>Anodonta hallenbeckii</i> Lea	1
** <i>Anodonta imbecillis</i> Say	105
<i>Anodonta marginata</i> Say	6
<i>Anodonta suborbiculata</i> Say	5
<i>Anodontooides ferussacianus</i> (Lea)	38
<i>Arcidens confragosus</i> (Say)	14
* <i>Lasmigona complanata</i> (Barnes)	3
** <i>Lasmigona compressa</i> (Lea)	25
<i>Lasmigona costata</i> (Raf.)	8
** <i>Lasmigona subviridis</i> (Conrad)	2
* <i>Strophitus rugosus</i> (Swainson)	64
<i>Strophitus undulatus</i> (Say)	9
	<u>479</u>
Lampsilinae (41 species; 14 genera)	
* <i>Actinonaias ellipsiformis</i> (Conrad)	206
<i>Carunculina corvunculus</i> (Lea)	6
** <i>Carunculina parva</i> (Barnes)	14
<i>Carunculina vesicularis</i> (Lea)	15
<i>Dysnomia compacta</i> (Lea)	1
<i>Dysnomia triquetra</i> (Raf.)	8
<i>Lampsilis anodontooides</i> (Lea)	10
<i>Lampsilis anodontooides floridensis</i> (Lea)	1
* <i>Lampsilis cariosa</i> (Say)	7
<i>Lampsilis claibornensis</i> (Lea)	27
<i>Lampsilis clarkiana</i> (Lea)	1
<i>Lampsilis dolabraeformis</i> (Lea)	5
<i>Lampsilis excavata</i> (Lea)	7
<i>Lampsilis fasciola</i> (Raf.)	44
<i>Lampsilis hydiana</i> (Lea)	6
<i>Lampsilis siliquoidea</i> (Barnes)	41
<i>Lampsilis siliquoidea rosacea</i> (DeKay)	18
<i>Lampsilis splendida</i> (Lea)	11
<i>Lampsilis subangulata</i> (Lea)	6
<i>Lampsilis tampicoensis</i> (Lea)	6
<i>Lampsilis ventricosa</i> (Barnes)	20
<i>Lampsilis ventricosa cohongoronta</i> (Ort.)	8
<i>Leptodea fragilis</i> (Raf.)	18
* <i>Leptodea laevissima</i> (Lea)	72
<i>Ligumia nasuta</i> (Say)	26
<i>Medionidus simpsonianus</i> Walker	9
<i>Obliquaria reflexa</i> Rafinesque	10
<i>Obovaria subrotunda</i> (Raf.)	3
<i>Plagiola lineolata</i> (Raf.)	5
* <i>Proptera alata</i> (Say)	14

Table 1 (contd.)

Species	Nos. sectioned
Lampsilinae (contd.)	
<i>Proptera purpurata</i> (Lamarck)	2
* <i>Ptychobranchnus fasciolaris</i> (Raf.)	22
* <i>Ptychobranchnus sublentum</i> (Say)	18
<i>Truncilla donaciformis</i> (Lea)	11
<i>Truncilla truncata</i> (Raf.)	1
<i>Villosa (Micromya) fabalis</i> (Lea)	4
* <i>Villosa (Micromya) iris</i> (Lea)	77
<i>Villosa (Micromya) lienosa</i> (Conrad)	11
<i>Villosa (Micromya) nebulosa</i> (Conrad)	4
<i>Villosa (Micromya) ogeecheensis</i> (Conrad)	9
<i>Villosa (Micromya) vibex</i> (Conrad)	17
	<u>801</u>
	1,871

*Occasionally hermaphrodites

**Dominantly hermaphrodites

3). Some of these species are discussed in the following. Data illustrating the gonadal picture in 27 specimens belonging to 23 species or forms are given in the legends to the figures.

I. Margaritanidae

Margaritifera margaritifera

(Linnaeus)

Fig. 4

This long-lived circumpolar pearl producing mussel is interesting in several respects. Comfort (1957) wrote: "If the 100-year estimate of longevity in *M. margaritifera* (L.) is correct, it is the longest-lived invertebrate known. A life span of this order in the wild would imply an exceedingly low adult mortality." Subsequently Hendelberg (1960) reported that the species could live, at least, 116 years. As already indicated, Schierholz (quoted by Pelseener, 1920) found 1 hermaphrodite among 80 specimens from northern Germany that he sectioned, while Hendelberg (1960) failed to find any in a series of 20 specimens from arctic Sweden.

In 1962 I collected *Margaritifera* from Pole Cat Creek in Yellowstone National Park, Wyoming, U.S.A. One of a series of 12 specimens sectioned was hermaphroditic (Fig. 4).

II. Unionidae

a. Unioninae

Paraffin sections were made of 567 specimens of this subfamily, representing 34 species. While none were found to be regularly hermaphroditic, 9 were found to be occasionally so, as detailed in Tables 1 and 3. Ortmann (1912) had already clearly stated that most of the Unioninae had separate sexes. He also noted that the gonadal tissues of these mussels were highly colored, showing various tints of orange, pink or bright crimson. While it has been stated that this coloring is associated with egg production, Ortmann's studies (: 244) would indicate that the color may be found in males as well as females. He asserts that there is "no relation of these colors to sex." My own observations corroborate his statement.

Fusconaia flava
(Rafinesque)
Figs. 8, 9

So far as I can determine, Sterki (1898) was the first and only one to indicate that this species "had a few acini producing ova in the gonad charged with copious sperm." The distinction, he explained, was particularly easy because of the bright crimson color of the ova. The animal's visceral mass indeed often shows a striking coloration. In the spring of 1962, a large collection of *Fusconaia flava* was made in the headwaters of the Grand River in Michigan. Some animals in this series were orange, others white. When an equal number of each were sectioned, the proportion of males and females was about equal, which tends to support the view that visceral coloration is not associated with sex. The hermaphroditic individuals figured were taken in 1959 and 1960 from Ore Creek, a tributary in the Saginaw drainage.

b. Anodontinae

In this subfamily 479 specimens representing 20 species were sectioned (Table 1). Of these, 8 species had hermaphroditic gonads: in 3 of these species or forms the condition was found to be dominant (Tables 1, 2); in the 5 others the condition is rare (Tables 1, 3). Four of the species showing hermaphroditism are discussed below.

Anodonta imbecillis Say⁴
Fig. 1

Again Sterki (1898) was the first to notice that all of the specimens of *Anodonta imbecillis* he examined were gravid. He found "ova and sperma in various proportions." The species is reported to be dominantly monoecious. It is also of interest that 3 characteristics, i.e., the hermaphroditic state, the lack of elevated umbones and the

supposed metamorphosis without parasitism, induced F. C. Baker (1927) to establish the genus *Utterbackia*. However, Mary Tucker (1928) showed clearly that *Anodonta imbecillis* does have a normal fish host, the green sunfish, *Apomotis cyanellus*.

Many years ago, (1940) I made serial sections of specimens of this species from the Ann Arbor, Michigan, area. It was evident that the acini composing the male elements were characteristically located along the sides of the visceral mass and were not as widely distributed as the acini containing the eggs. More recently I examined animals considered to belong to this same species, from Hillsboro River in Florida. It came somewhat as a surprise to find that the sexes of that population were separate. In a recent paper, Johnson (1965) reports a hitherto unrecognized species of *Anodonta*, which he calls *A. peggyae*, also giving Hillsboro River as one of the localities. This report suggests that the difference in the sexual condition observed between the northern and southern forms, thought to be one of geographical strain, might even be specific, a moot point. Johnson, incidentally, corrects the spelling of the specific name *imbecillis* to *imbecilis*.

Anodonta grandis footiana (Lea)
Fig. 15

Observations by Boycott and Oldham led Bloomer (1930, 1934, 1935, 1939) to extensively investigate the sex conditions of *Anodonta cygnea* (L.) in the British isles. From the structure of the gonad he suspected possible sex reversal (1934). Studying the ratios of males, females and hermaphrodites in various populations (1939) he found these constant for, but varying between, populations. His stimulating papers aroused our curiosity and our interest in *Anodonta grandis* Say, the most common North American species, about which, in contrast to *A. imbecillis*, no information was available. As reported by van der Schalie & Locke (1941), gonads of a lake form of this species, *A. grandis footiana* were sectioned and hermaphroditism was

⁴The related species *Anodonta henryana* Lea and *A. gibbosa* Say have not been sectioned in this study, but from preliminary examination it would seem that they are not monoecious.

TABLE 2. The only North American naiades in which hermaphroditism is the dominant condition

Families	Species
MARGARITANIDAE	none
UNIONIDAE:	
Unioninae	none
Anodontinae	<i>Anodonta imbecillis</i> Say (Fig. 1) <i>Lasmigona compressa</i> (Lea) (Fig. 2) <i>Lasmigona subviridis</i> (Conrad)
Lampsilinae	<i>Carunculina parva</i> (Barnes) (Fig. 3)

TABLE 3. Species of North American naiades in which hermaphrodites were occasionally found

MARGARITANIDAE	
	<i>Margaritifera margaritifera</i> (Linn.) (Fig. 4)
UNIONIDAE	
Unioninae	
	<i>Elliptio dilatatus</i> (Raf.) (Figs. 5, 6)
	<i>Elliptio productus</i> (Conrad) (Fig. 7)
	<i>Fusconaia flava</i> (Raf.) (Figs. 8, 9)
	<i>Fusconaia ebenus</i> (Lea)
	<i>Gonidea angulata</i> (Lea) (Fig. 17)
	<i>Pleurobema cordatum</i> (Raf.)
	<i>Pleurobema cordatum coccineum</i> (Conrad) (Figs. 10, 11)
	<i>Quadrula quadrula</i> Raf.
	<i>Tritogonia verrucosa</i> (Say) (Fig. 12)
Anodontinae	
	<i>Alasmidonta marginata</i> (Say) (Figs. 13, 14)
	<i>Anodonta corpulenta</i> Cooper (Fig. 16)
	<i>Anodonta grandis footiana</i> (Lea) (Fig. 15)
	<i>Lasmigona complanata</i> (Barnes) (Fig. 18)
	<i>Strophitus rugosus</i> (Swainson) (Fig. 19)
Lampsilinae	
	<i>Actiononaias ellipsiformis</i> (Conrad) (Figs. 20, 21)
	<i>Lampsilis cariosa</i> (Say) (Fig. 22)
	<i>Leptodea laevissima</i> (Lea) (Fig. 23)
	<i>Proptera alata</i> (Say) (Fig. 24)
	<i>Ptychobranchus fasciolaris</i> (Raf.) (Fig. 25)
	<i>Ptychobranchus subtentum</i> (Say) (Fig. 26)
	<i>Villosa (Micromya) iris</i> (Lea) (Fig. 27)

FIGS. 1 - 9. Gonadial tissues of some North American naiades showing various degrees of hermaphroditism (stain: haematoxylin and eosin).

FIG. 1. *Anodonta imbecillis* (Say). Huron River, above Ypsilanti, Washtenaw Co., Michigan. May 25, 1940. Henry van der Schalie, Collector. Specimen: 5 years old. Normal hermaphrodite with male and female tissues separated so that male gonad is found along the upper and outer sides of the visceral mass. (Original photomicrograph taken at X 100).

FIG. 2. *Lasmigona compressa* (Lea). Ore Creek, 5 mi. below Hartland, Michigan. June 9, 1959. Henry van der Schalie, Collector. Specimen: 82 mm long, 5 years old, gravid. A typical and normal hermaphrodite with eggs in one follicle and sperm developed in another. (Taken at X 125).

FIG. 3. *Carunculina parva* (Barnes). Tennessee River, Station 3, near New Johnsonville, Tennessee. October 16, 1964. John M. Bates, Collector. Specimen: 27.5 mm long, 8 years old, not gravid. A normal hermaphrodite with male and female follicles separate. (Taken at X 125).

FIG. 4. *Margaritifera margaritifera* (L.). Pole Cat Creek, just south of Yellowstone Park, Wyoming. August 15, 1962. Henry van der Schalie, Collector. Specimen: 34 mm long, 5 years old, not gravid. Note that male and female follicles are separate. (Taken at X 125).

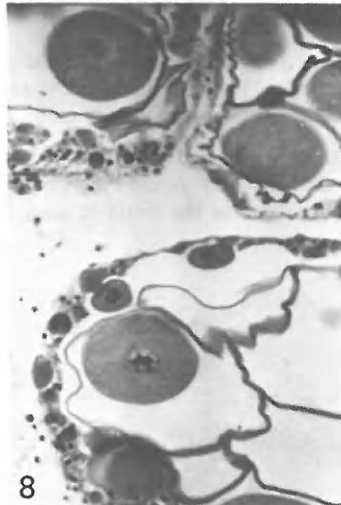
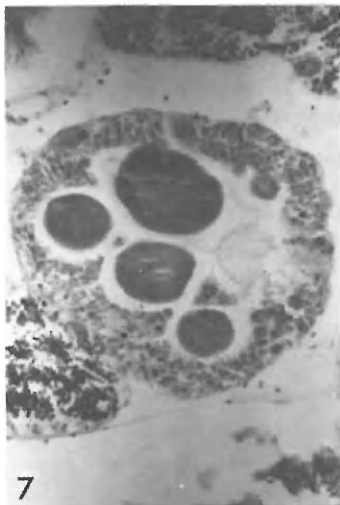
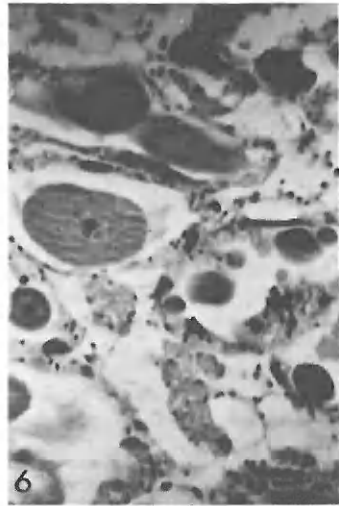
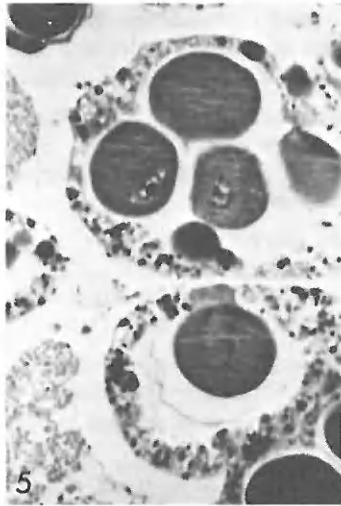
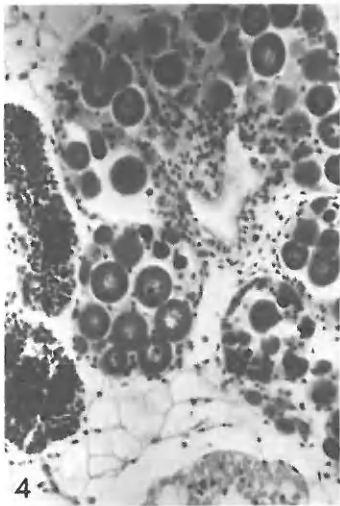
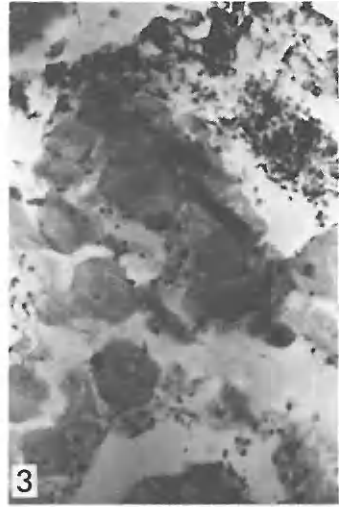
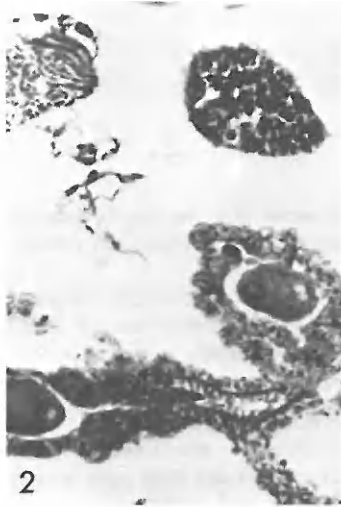
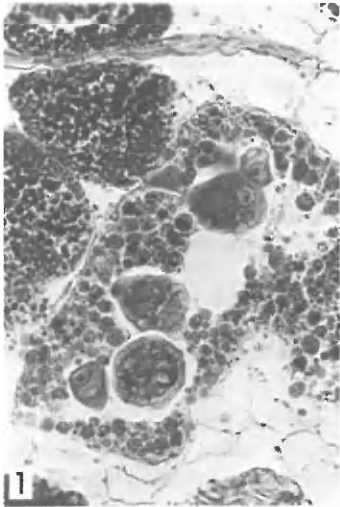
FIG. 5. *Elliptio dilatatus* (Raf.). Cranberry Creek, Byron, Shiawassee Co., Michigan. June 5, 1961. Henry van der Schalie, Collector. Specimen: 67 mm long, 8 years old, not gravid. Mainly female, but with male tissue developing in female follicles; eggs seem to be developing normally. (Taken at X 125).

FIG. 6. *Elliptio dilatatus* (Raf.). French Creek, trib. Allegheny River, 5 mi. north of Meadville, Pennsylvania. July 17, 1961. MacKenzie Keith, Collector. Specimen: 4 years old, 61 mm long, gravid. Spermatogenesis clearly evident in female follicles. (Taken at X 125).

FIG. 7. *Elliptio productus* (Conrad). Savannah River, above Route 301 bridge, south of Allendale, S. Carolina. June 24, 1964. John M. Bates, Collector. Specimen: 59 mm long, 6 years old, not gravid. A small amount of normal female tissue present in a preponderantly male specimen. (Taken at X 125).

FIG. 8. *Fusconaia flava* (Raf.). Ore Creek, 1 mi. northwest of Hartland, Livingston Co., Michigan. May 22, 1960. Henry van der Schalie, Collector. Specimen: 74 mm long, 12 years old, not gravid. A female with only a small amount of spermatogenesis in wall of follicles. (Taken at X 125).

FIG. 9. *Fusconaia flava* (Raf.). Ore Creek at Clyde Road, below Hartland, Livingston Co., Michigan. June 25, 1959. Henry van der Schalie, Collector. Specimen: 68 mm, 11 years old, not gravid; predominantly male with only small foci of female tissue and eggs tending to be suppressed. (Taken at X 100).



FIGS. 10-18. Gonadial tissues of some North American naiades showing various degrees of hermaphroditism (stain: haematoxylin and eosin).

FIG. 10. *Pleurobema cordatum coccineum* (Conrad). South branch Cranberry Creek at Byron, Shiawassee Co., Michigan. Nov. 21, 1960. Henry van der Schalie, Collector. Specimen: 35 mm long, 3 years old, not gravid; mostly female tissue with only a small amount of discrete male follicles. (Original photomicrograph taken at X 100).

FIG. 11. *Pleurobema cordatum* (Raf.). Tennessee River, above New Johnsonville, Tennessee. Nov. 11, 1963. John M. Bates, Collector. Specimen: 80 mm long, 17 years old, not gravid; appears to be about half male and half female with eggs poorly developed in follicles with spermatogenesis in walls. (Taken at X 100).

FIG. 12. *Tritogonia verrucosa* (Raf.). Guadalupe River, 1/2 mi. west of Sequin, Guadalupe Co., Texas. August 22, 1962. John M. Bates, Collector. Specimen: 66 mm long, 5 years old, not gravid; mainly female with patches showing spermatogenesis. (Taken at X 125).

FIG. 13. *Alasmidonta marginata* (Say). River Raisin, Sharon Hollow, Washtenaw Co., Michigan. July 20, 1962. Henry van der Schalie, Collector. Specimen: 41 mm long, 3 years old, not gravid; evidently a female with patches of sperm developing in walls of follicles; eggs do not seem normal in development. (Taken at X 125).

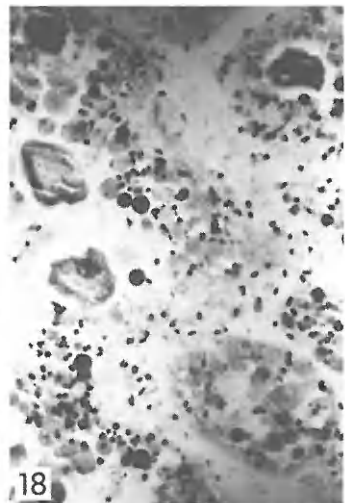
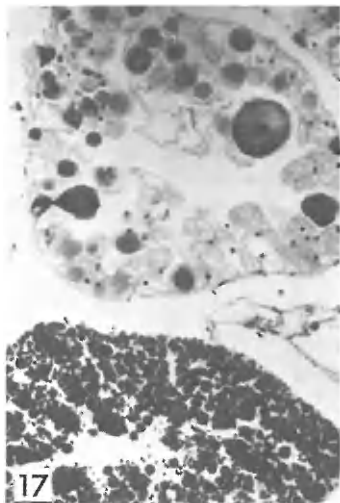
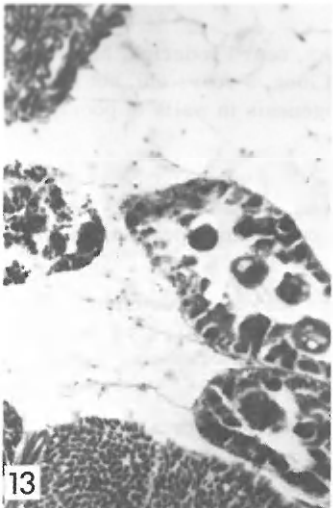
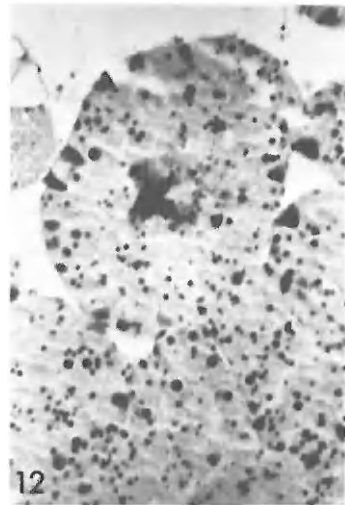
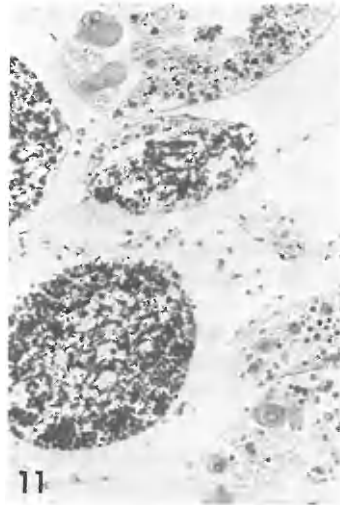
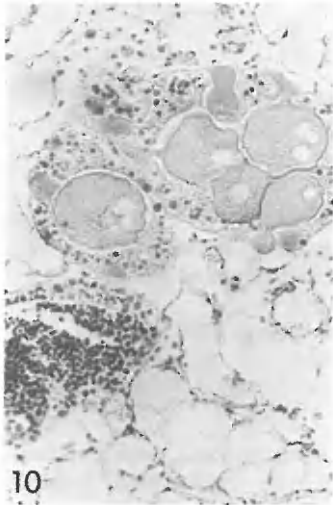
FIG. 14. *Alasmidonta marginata* (Say). Powell River, at U. S. 25 E, Claiborne Co., Tennessee. June 23, 1961. B. Dazo and H. van der Schalie, Collectors. Specimen: 62 mm long, 10 years old, not gravid; evidently sex quite mixed so that many egg follicles have spermatogenesis in walls with eggs often suppressed in development. (Taken at X 125).

FIG. 15. *Anodonta grandis footiana* (Lea). Zukey Lake, Lakeland, Livingston Co., Michigan. May 11, 1940. Henry van der Schalie, Collector. Specimen: 7 years old; mostly male with only small amount of female tissue which seems to be normal in development. (Taken at X 125).

FIG. 16. *Anodonta corpulenta* Cooper. Tennessee River, slough along river at mile 97.7, near New Johnsonville, Tennessee. October 16, 1964. John M. Bates, Collector. Specimen: 81 mm long, 5 years old, gravid; eggs do not appear to be developing normally and spermatogenesis appears in walls of some follicles. (Taken at X 125).

FIG. 17. *Gonidea angulata* (Lea). Snake River, near Bliss, Idaho. August 18, 1962. Henry van der Schalie, Collector. Specimen: 117 mm long, 15 years old, not gravid; a typical hermaphrodite with both male and female tissues well developed. (Taken at X 125).

FIG. 18. *Lasmigona complanata* (Barnes). River Rouge, Michigan. October 1, 1962. Carol Geake, Collector. Specimen: 170 mm long, 12 years old, gravid; the gonad appears to be mostly female but with scattered spermatogenesis in the walls of many follicles. (Taken at X 125).



FIGS. 19-27. Gonadial tissues of some North American naiades showing various degrees of hermaphroditism (stain: haematoxylin and eosin).

FIG. 19. *Strophitus rugosus* (Swainson). Inlet to Zukey Lake, Livingston Co., Michigan. July 14, 1960. Bonifacio Dazo, Collector. Specimen: 56 mm long, 4 years old, gills not clear as to gravid state; mostly male with only a small amount of female tissue. (Original photomicrograph taken at X 125).

FIGS. 20 & 21. *Actinonaias ellipsiformis* (Conrad). Ore Creek, at Clyde Road, near Hartland, Livingston Co., Michigan. Henry van der Schalie, Collector. Specimen: 67 mm long, 10 years old, not gravid; one of most unusual hermaphrodites observed in that male and female tissues quite thoroughly mixed. (Taken at X 125).

FIG. 22. *Lampsilis cariosa* (Say). Potomac River, Point of Rocks, near Frederick, Maryland. September 22, 1962. John M. Bates, Collector. Specimen: 100 mm long, 8 years old, not gravid; eggs in poor development but in discrete follicles; some spermatogenesis in walls of poorly developed female follicles. (Taken at X 125).

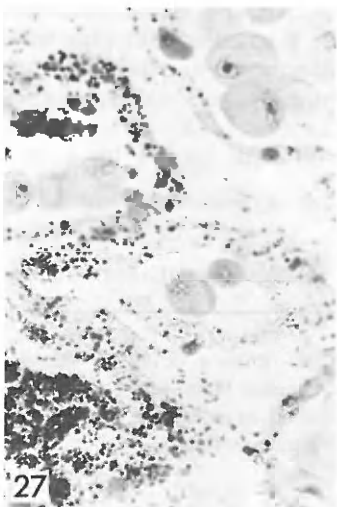
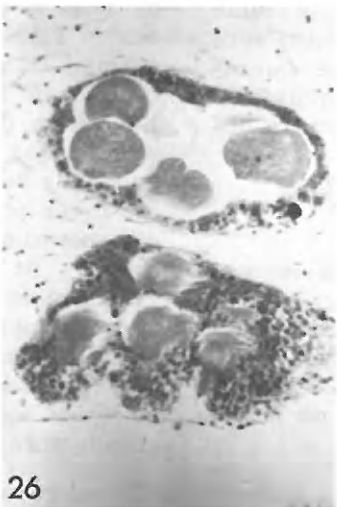
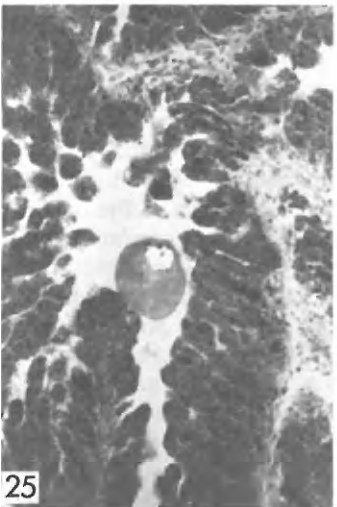
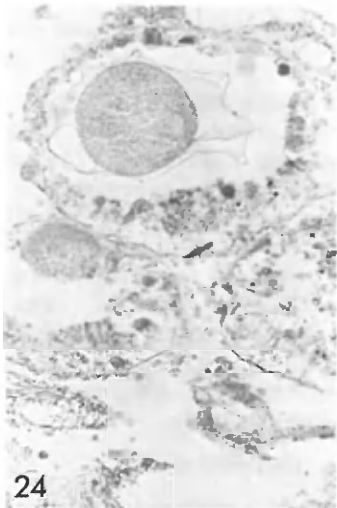
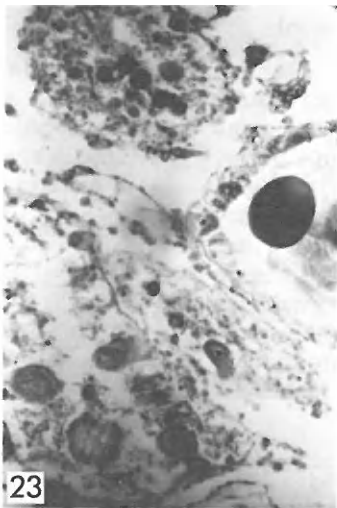
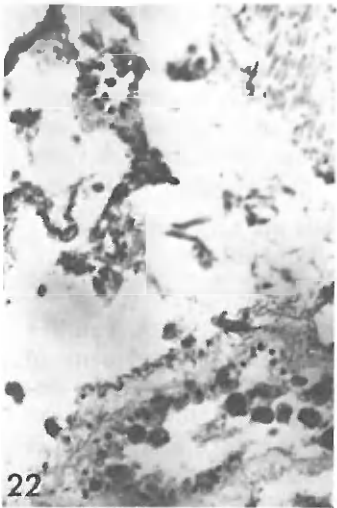
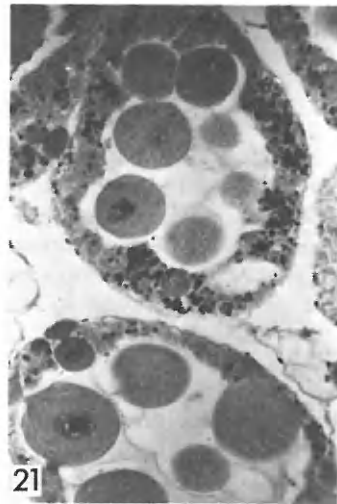
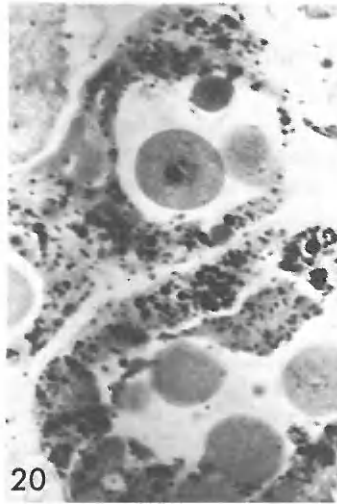
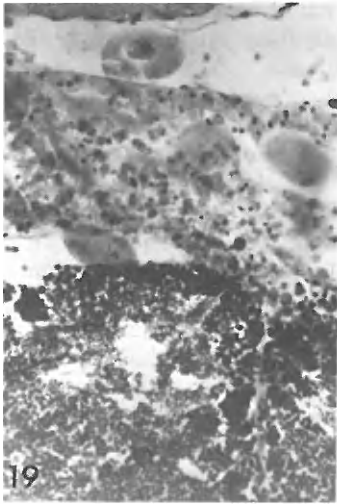
FIG. 23. *Leptodea laevissima* (Lea). Tennessee River, at mile 97.7 near New Johnsonville, Tennessee. October 16, 1964. John M. Bates, Collector. Specimen: 55 mm long, 3 years old, gravid; mostly female but with small foci of what appears to be developing sperm. (Taken at X 125).

FIG. 24. *Proptera alata* (Say). Lake Erie, at 32 feet depth near Middle Sister Island, Ohio. August 22, 1962. Yarl Hiltunen, Collector. Specimen: 66 mm long, 5 years old, gravid; mainly female tissue but with a hermaphroditic trend shown by an incipient spermatogenesis. (Taken at X 100).

FIG. 25. *Ptychobranchnus fasciolaris* (Raf.). Little Portage River, above Toma Road, Washtenaw Co., Michigan. Bonifacio Dazo, Collector. Specimen: 69 mm long, 9 years old, gravid; mainly female but with small areas of spermatogenesis scattered throughout the glandular masses. (Taken at X 125).

FIG. 26. *Ptychobranchnus subtentum* (Say). Powell River, at U. S. 23 E, Claiborne Co., Tennessee. August 23, 1961. B. Dazo and H. van der Schalie, Collectors. Specimen: 82 mm long, 15 years old, not gravid; a female with clear-cut patches of male tissue with follicles showing poor development of eggs. (Taken at X 125).

FIG. 27. *Villosa (Micromya) iris* (Lea). River Raisin, Sharon Hollow, Washtenaw Co., Michigan. July 20, 1962. Norman Reigle, Collector. Specimen: 33 mm long, 3 years old; female with gills about spent; mainly female, but with unusually abundant spermatogenesis appearing in walls of many female follicles. (Taken at X 100).



demonstrated in 2 out of 14 specimens.

Lasmigona compressa (Lea) and
L. subviridis (Conrad)

Fig. 2

All 25 specimens of *Lasmigona compressa* collected from several creeks in Michigan were hermaphroditic. This species is widespread and unique in that it is able to occupy very minute creeks and streams—places in which often no other mussels are found.

A closely related eastern species of similar ecology, *L. subviridis*, has also been found for the first time to be dominantly hermaphroditic (2 out of 2 examined). The relationship of these 2 species is uncertain.

Strophitus rugosus (Swainson)

Fig. 19

Among others, a series of 64 specimens was collected in a creek connecting 2 lakes in Livingston County, Michigan, in every month of the year. The hermaphroditic condition was observed in only 1 specimen. There was a clear-cut separation between the male and female tissues. The animal was collected on July 14, 1960, and there were sufficient eggs in a normal state to indicate that the specimen was a functional hermaphrodite.

c. Lampsilinae

In this subfamily 801 specimens representing 41 species were sectioned (Table 1); 8 species belonging to 7 genera were found to be hermaphroditic; one, *Carunculina parva* was regularly ambisexual (Tables 1, 2) and 7 species were occasionally so (Tables 1, 3).

Carunculina parva (Barnes)⁵

Fig. 3

Hermaphroditism in this species was

reported at an early date (Sterki, 1898). Tepe (1943) carefully studied the histology of the gonads. He reported the occasional presence of hermaphroditic acini that contained eggs as well as sperm and made the following statement regarding this condition:

"In most instances it was observed that eggs enclosed in male follicles were smaller (20-24 microns) than eggs from strictly female follicles (40-100 microns). The eggs in essentially male follicles were free from germinal epithelium, and their small size does not seem to indicate immaturity. Both eggs and spermatozoa appeared mature in all the individuals, which would seem to indicate that this hermaphroditic condition does not represent a phase in a periodic sex reversal."

Our studies on 14 individuals from the Tennessee River show essentially the same conditions. All individuals examined were hermaphrodites; 2 of them also had acini with both eggs and sperm.

Actionaias ellipsiformis
(Conrad)

Figs. 20, 21

In an earlier study (H. & A. van der Schalie, 1963) some 200 specimens of this species were collected over an extended period. It was found that the gonads remained undifferentiated for the first 2 years. All specimens 2 years old or older were either distinctly male or female, except for one hermaphrodite. This specimen was the largest (68 mm) of a series of 25 individuals taken late in June from Ore Creek, Livingston Co., Michigan, of which 13 were gravid and 12 non-gravid. It was originally considered a female because the lower posterior portion of the outer gill showed a small amount of marsupial tissue. At that time the animal was reaching the end of the spring glochidial shedding period, but there was enough gill modification to show it was functioning as a female. Its hermaphroditic condition was not discovered until the gonads were sectioned, when it was found

⁵Two other species of *Carunculina*, *C. corniculatus* (Lea) and *C. vesicularis* (Lea), collected in southern states, were not found to be monoecious.

that male and female tissue was quite thoroughly mixed.⁶ This mussel, with 10 annuli on the shell, was the oldest of the series. On the chance that this hermaphroditic condition might be associated with senescence, the other large specimens of this series were re-examined, but results were negative.

Villosa (Micromya) iris (Lea)

Fig. 27

A specimen of this species has also been found to have similarly mixed gonad tissue,⁶ simultaneously producing eggs and sperm.

DISCUSSION

Hermaphroditism in mollusks is supposed to be derived from an originally dioecious condition. Some authors emphasize that the condition tends to appear in situations when the animal is confronted with difficulties in its normal reproductive activity. Hence hermaphroditism might be an adaptive mechanism, giving the species some evolutionary advantage.

Now that almost 100 North American naiad species have been studied, it has become evident that among this large and highly evolved group relatively few are regularly hermaphroditic. Essentially the situation is similar to that in the marine lamellibranchs in which also there are comparatively few species that are monoecious. Among the naiades, only the Anodontinae and the Lampsilinae appear to have species in which the condition occurs regularly and only 4 species are involved: 3 in the former subgenus and 1 in the latter. All of the sporadic cases that were detected in 22 species or forms clearly belong to the

category that Coe (1943: 156) considered as accidental or developmental ambisexuality. Under this heading he stated:

"Even in species which are otherwise strictly of separate sexes there may be an occasional individual with functional hermaphroditism. These can all be considered as resulting from deviations in the developmental processes due to a failure of the sex-differentiating mechanism to function normally. The proportion of spermatogenic and ovogenic tissues in the gonad is highly variable, some individuals having approximately equal parts of both sexual types, while others are principally one sex, with but few cells characteristic of the opposite sex. This type of sexuality is more common in the pelecypods than in most other groups of animals and it occurs frequently in young individuals at the first reproductive season. In certain local races of oviparous oysters, clams and mussels it is possible to determine whether the initial sexual phase is normal or accidental."

In the present study specimens from species found to be regularly hermaphroditic presented a "normal" histological picture, with male and female tissues, resp. acini separate, a situation that was also encountered in *Margaritana*, *Strophitus* and *Gonidea*. The other occasional hermaphrodites, however, were as a rule predominantly of one sex, with only some tissue or cells of the other sex developing in or among the follicles of the dominant sex.

The various occasional hermaphrodites detected were certainly not restricted to, or prevalent in, young individuals. But Coe does not quote only age as a factor connected with modification of the sexual state. Temperature, resp. season, and several other factors have also been incriminated. Thus, for instance, nutritional disturbances of the Bombay oyster apparently resulted in an increased proportion of males, whereas in years and locations favoring rapid growth, Virginia oysters had a large proportion of females. Habitat has been

⁶The unusual condition of the gonads of the 2 specimens here quoted has been recently discussed (van der Schalie, 1969). It was stressed that the simultaneous production of eggs and sperm is quite uncommon among freshwater mussels.

considered to play a role: Weisensee (1916: 292) claimed to have observed that the dioecious condition was normal for *Anodonta cygnea* living in rivers, while those living in impounded waters tended to be hermaphroditic.

In other instances variation is attributed to heredity per se: Coe (1943) reports races with different heredity in the Virginia oyster. Bloomer (1939) reports populations of *Anodonta cygnea* in which hermaphroditism was relatively more common than in others in a constant manner. From the findings reported in this survey, it appears quite possible that wide-ranging species, such as *Anodonta imbecillis*, may not be hermaphroditic throughout their whole range, so that northern forms may differ in this respect from the southern representatives (? *A. peggyae*). Such a regional difference was recently shown to exist (van der Schalie, 1965) in a freshwater gastropod, *Campeloma*, which in the northern United States is parthenogenetic, no males being known from that region.

Though interesting to speculate on, Weisensee's contention as to a direct influence of the environment would, according to his own testimony, need much additional investigation before it could be plausibly substantiated. Although a wide cross-section of the North American mussel fauna has now been sampled, including mussels living in streams as well as in lakes, it has not been possible so far to demonstrate any environmental factor that would indicate any causal relation with sexuality. The extent of ambisexuality and the mechanisms producing it still remain open questions. Studies would need to be intensified so as to cover species in greater detail, i. e., at different ages, seasons and localities. Such investigations are not easy because gonad smears or sections must be made to discover hermaphroditism and ample material must be procured. While it would be of interest to explore factors (chemical, physical, etc.) that might perhaps serve to induce sex

changes in the naiades, this group unfortunately does not lend itself readily to laboratory experiments. However, investigations are continuing. Arrangements have been made for the procurement of *Margaritana* from the Rocky Mountain regions of the U.S.A. during the active season of the year, and a study to determine the sex ratios of several commercially important mussels is being conducted by the University of Michigan in Kentucky Lake, Tennessee, and in the Muskingum River in Ohio.

ACKNOWLEDGEMENTS

Several of our staff and students assisted with preparing the thousands of paraffin blocks and cutting thin sections that made this investigation possible. Some of the sections were made by my wife, Annette; others were made by Khan Tandaraporn, Barbara Peckham, Susanne Pauly, Jane Phelps and Paula Levy. Colleagues and students generously contributed live specimens for proper fixation and preservation; among them mention should be made especially of John M. Bates, William H. Heard, Bonifacio Dazo and Robert Wakefield. The photographs were made with the assistance of Vera Farris, Louis P. Martonyi and Gene K. Lindsay.

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RÉSUMÉ

L'HERMAPHRODISME CHEZ LES MOULES D'EAU DOUCE
D'AMÉRIQUE DU NORD

H. van der Schalie

Les informations sur l'existence de l'hermaphrodisme parmi les moules d'eau douce de la riche faune des U.S.A., sont fragmentaires. Dans cette étude, les gonades de 1871 exemplaires appartenant à 97 espèces et 32 genres ont été examinées histologiquement, par la technique des coupes à la paraffine. Seulement 4 espèces parmi 2 sous-familles des unionides se sont montrées essentiellement hermaphrodites (monoïques); 3 chez les Anodontinae: *Anodonta imbecillis*, *Lasmigona compressa* et (espèce toute proche) *L. subviridis*; 1 chez les Lampsilinae: *Carunculina parva*.

Des hermaphrodites accidentels ont été trouvés chez 22 autres espèces ou formes, appartenant à 17 genres et 2 familles. En général, de tels individus ont généralement un sexe dominant, avec seulement une faible quantité de tissus de l'autre sexe. Un spécimen ambisexe a été trouvé chez les Margaritanidae, chez *Margaritifera margaritifera*, parmi 24 spécimens sectionnés représentant 2 genres et espèces. Chez les Unionidae, des hermaphrodites accidentels se rencontrent dans les 3 sous-familles. Parmi les Unioninae, sur 567 spécimens (34 espèces, 11 genres) examinés, de tels individus ont été trouvés dans 9 espèces (ou formes) et 5 genres, soit: *Elliptio dilatatus*, *E. productus*, *Fusconaia ebenus*, *F. flava*, *Gonidea angulata*, *Pleurobema cordatum*, *P. c. coccineum*, *Quadrula quadrula* et *Tritogonia verrucosa*. Parmi les Anodontinae, sur un total de 479 spécimens (20 espèces, 5 genres) sectionnés, des hermaphrodites accidentels ont été mis en évidence chez 5 espèces appartenant à 5 genres, dont 2 sont des genres comportant aussi des espèces hermaphrodites; c.a.d. qu'ils se rencontrent chez: *Anodonta corpulenta*, *A. grandis footiana* et *Lasmigona complanata* ainsi que chez *Alasmidonta marginata* et *Strophitus rugosus*. Chez les Lampsilinae, avec un total de 801 spécimens (41 espèces, 14 genres) sectionnés, le phénomène a été à nouveau trouvé chez 7 espèces représentant 6 genres, c.a.d. chez: *Actinonaias ellipsiformis*, *Lampsilis cariosa*, *Leptodea laevissima*, *Proptera alata*, *Ptychobranthus fasciolaris*, *P. subtentum* et *Villosa (Micromya) iris*.

Ce relevé, à peu près complet des moules d'eau douce américaines, montre qu'elles sont généralement dioïques. La question reste toujours posée de savoir, si oui ou non, l'hermaphrodisme apparaît chez des animaux placés dans des conditions de milieu difficiles, comme cela a été antérieurement suggéré.

A. L.

RESUMEN

HERMAFRODITISMO EN ALMEJAS DE AGUA DULCE
DE NORTE AMERICA

H. van der Schalie

La información existente acerca de la amplitud del hermafroditismo en la rica fauna de naiades de U.S.A. es fragmentaria. Para el presente estudio se examinaron las gonadas de 1871 ejemplares pertenecientes a 97 especies de 32 géneros, usando cortes de bloques de parafina. Sólo 4 especies, en dos subfamilias de uniónidos, mostraron ser predominantemente hermafroditas (monoicos); 3 en los Anodontinae: *Anodonta imbecillis*, *Lasmigona compressa* y (la estrechamente emparentada) *L. subviridis*, y 1 en los Lampsilinae: *Carunculina parva*.

En otras 22 especies o formas, pertenecientes a 17 géneros y 2 familias, se encontraron hermafroditas esporádicos. Usualmente estos individuos parecen ser predominantemente de un sexo, con sólo una pequeña cantidad de tejido gonadal del sexo opuesto. Un ejemplar ambisexual se encontró en Margaritidae, en *Margaritifera margaritifera*, entre 24 ejemplares seccionados que representaban 2 géneros y especies. En los Unioninae, individuos accidentalmente monoicos aparecieron en las 3 subfamilias. Entre los Unioninae con 567 ejemplares (34 especies, 11 géneros) examinados, tales individuos se encontraron en 9 especies (o formas) de 6 géneros: *Elliptio dilatatus*, *E. productus*, *Fusconaia ebenus*, *F. flava*, *Gonidea angulata*, *Pleurobema cordatum*, *P. c. coccineum*, *Quadrula quadrula*, y *Tritogonia verrucosa*. En los Anodontinae, con un total de 479 ejemplares (20 especies, 5 géneros) seccionados, hermafroditas esporádicos se mostraron en 5 especies de 4 géneros, de los cuales 2 géneros son los que también contenían las especies predominantemente hermafroditas; las 5 especies son: *Anodonta corpulenta*, *A. grandis footiana*, *Lasmigona complanata*, *Alasmidonta marginata* y *Strophitus rugosus*. En los Lampsilinae con un total de 801 especímenes (41 especies, 14 géneros) seccionados, la condición fue detectada en otras 7 especies representantes de 6 géneros: *Actinonaias ellipsiformis*, *Lampsilis cariosa*, *Leptodea laevisissima*, *Proptera alata*, *Ptychobranchus fasciolaris*, *P. subternum* y *Villosa (Micromya) iris*.

Esta inspección de un carácter más bien extensivo de los naiades americanos, muestra que ellos son generalmente dioicos. Queda aun por resolver la cuestión si el hermafroditismo aparece o no en los animales que confrontan condiciones ambientales difíciles.

J. J. P.

АБСТРАКТ

ГЕРМАФРОДИТИЗМ У СЕВЕРО-АМЕРИКАНСКИХ ПРЕСНОВОДНЫХ МОЛЛЮСКОВ

Г. ВАН-ДЕР ШЕЙЛИ

О гермафродитизме среди пресноводных наяид, фауна которых в США очень богата, известно очень мало. В настоящей статье рассматриваются результаты гистологического изучения гонад этих моллюсков, полученных от 1871 экземпляра 97 видов из 32 родов. Для срезов использовались парафиновые блски.

Лишь 4 вида из 2 подсемейств унионид были преимущественно гермафродитными (однодомными). Это 3 вида из Anodontinae: *Anodonta imbecillis*, *Lasmigona compressa* и близкородственный *L. subviridis* и один вид из Lampsilinae *Carunculina parva*.

Спорадический гермафродитизм был отмечен у 22 видов или форм, относящихся к 17 родам и 2 семействам. Обычно такие особи с виду кажутся однополыми, лишь с небольшой частью гонады противоположного пола. Одна двуполовая особь была найдена среди Маргаритинид- *Margaritifera margaritifera*, из 24 экземпляров, на которых были сделаны срезы, представляют 2 вида и вида. Из Unionidae случайно однодомные особи были встречены во всех трех подсемействах. Среди просмотренных 567 экземпляров (34 вида и 11 родов) такие особи были найдены у 9 видов (или форм) из 5 родов. Это: *Elliptio dilatatus*, *E. productus*, *Fusconaia ebenus*, *F. flava*, *Gonidea angulata*, *Pleurobema cordatum*, *P. c. coccineum*, *Quadrula quadrula* и *Tritogonia verrucosa*.

Из 479 изученных экземпляров Anodontinae (20 видов и 5 родов), спорадический гермафродитизм был отмечен у 5 видов из 4 родов. Из них 2 относились к родам, также имеющим преимущественно гермафродитные виды. Это: *Anodonta corpulenta*, *A. grandis footiana* и *Lasmigona complanata*, а также *Alasmidonta marginata* и *Strophitus rugosus*. Из Lampsilinae был изучен 801 экземпляр (41 вида из 14 родов); указанные выше особенности отмечены у 7 видов из 6 родов, а именно: *Actinonaias elipsiformis*, *Lampsilis cariosa*, *Leptodea laevissima*, *Proptera alata*, *Ptychobranthus fasciolaris*, *P. subtentum* и *Villosa (Micramya) iris*.

Эти довольно экстенсивные исследования американских наяид показали, что они являются преимущественно раздельнополыми. Вопрос о том, появляется ли гермафродитизм у животных в трудных условиях существования, остается пока открытым.

Z. A. F.